African Invertebrates Vol. 44 (2) Pages 191–201 Pietermaritzburg December, 2003

A redescription of *Isalomyia irwini* Stuckenberg, the wormlion fly of Madagascar, related to an Arabian species for which the new genus *Alhajarmyia* is erected (Diptera: Vermileonidae)

by

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ABSTRACT

New material of the Madagascan vermileonid *Isalomyia irwini* Stuckenberg, 2002 enables a more complete description to be given. This species has exceptional apomorphies in the structure of its head and proboscis; the antennae also are highly modified, and share unique synapomorphies with an Omani species previously named *Lampromyia umbraticola* Stuckenberg & Fisher, 1999. A reassessment of relationships suggests that *irwini* and *umbraticola* are sister-groups. Grounds for the original inclusion of *umbraticola* in the genus *Lampromyia* Macquart, 1835 are now known to be invalid, and a new genus, *Alhajarmyia*, is erected for this species. Biogeographical implications of the relationship between these Arabian and Madagascan taxa are discussed. Aerial transport between Madagascar and East Africa, assisted by intermediate islands, could have occurred, and an East African centre of an ancestral form seems plausible.

INTRODUCTION

The Madagascar fauna is renowned for its endemicity and the often enigmatic biogeographical relationships of its endemic taxa. The recent discovery of the first vermileonid species on the island, *Isalomyia irwini* Stuckenberg, 2002, was thus of particular interest. Vermileonidae appear to be a phylogenetically isolated lineage in the homeodactylous Brachycera; the family is currently segregated in its own infraorder, the Vermileonomorpha (Griffiths 1994; Stuckenberg 2001). The biogeography of Vermileonidae is becoming better understood, and its division into Laurasian and Gondwanan components is now evident (Stuckenberg 2001). When *Isalomyia* was described on a female specimen, it was recognised immediately as a member of the Gondwanan clade, although no further assessment of relationships could be made. Now, thanks to the persistence of Dr M. E. Irwin who discovered this vermileonid in the Isalo National Park, many additional specimens are available from the type locality, including the first males. Evidence has been found that its sister-group is a species from the Hajar Mountains in Oman. This revealed the need for a revised classification of that Arabian species, and a new genus is erected for it. *Isalomyia irwini* has been found to have remarkable modifications of the head and mouthparts. Transformation trends seen in other afrotropical vermileonid lineages have been extended in this species, resulting in unique adaptations probably associated with some special feeding mode.

TERMINOLOGY

Standard morphological terminology is used; naming of wing veins follows McAlpine (1981). The term *syntrophium*, introduced by Jobling (1976), is applied to the compound mouthpart structure constituted collectively by the labrum, hypopharynx and laciniae, and the mandibles if present. Terminology of antennal components follows Stuckenberg

(1999): the primitive brachycerous flagellum with eight segments is referred to as the *style*; when basal segments have fused, the resulting compound structure is the *postpedicel*, and the remaining free stylomeres constitute a modified style. The median adhesive pad between the tarsal claws is the *mediolobus*, following Röder (1986). The ventral component of the hypopygium formed by the fused basistyles and ninth sternite is called the *synsternite*. The *dorsal bridge* is a dorsobasal sclerite extending across the gap between the upper margins of the synsternite, to which the epandrium is attached above and from which the aedeagus is suspended below. T = tergite, S = sternite. Nomenclature of sclerotised structures around the occipital foramen is not standardised in the literature. The term *paragular sclerites* is adopted from Crampton (1942) for the small sclerites bordering the foramen laterally; these are termed 'parapostgenae' by Peterson (1916), and 'postocciput' by Chassagnard & Tsacas (1974). The term *parocciput* is taken from Peterson (1916); following Bromley (1926), it is restricted to an unpaired, median, visor-like projection at the dorsal perimeter of the occipital foramen. Label data are cited verbatim, a slash (/) indicating the end of a line.

SYSTEMATICS

Genus *Isalomyia* Stuckenberg

Isalomyia Stuckenberg, 2002: 3. Type species *Isalomyia irwini* Stuckenberg, 2002: 3; monotypic and by original designation.

Diagnosis: Basal section of labium recurved within head capsule; a single, unforked pseudotrachea in each labellum; paragular sclerites exposed in lateral view; stipital sclerites converging posteriorly and fusing over about half of their length; spermatheca mushroom-shaped, with proximal concavity in which duct is inserted, and a central aperture on distal surface through which an eversible membranous sac is extrudable. Mediolobus vestigial.

Supplementary description: *Antennae* (Figs 4, 5) large, carried semi-erect, sexually dimorphic; plesiomorphic segmentation retained, eight stylomeres present; male stylomeres (Fig. 4) strongly flattened laterally, thin in dorsal view, profile of upper edge more strongly curved than lower edge, stylomeres gradually decreasing in depth; penultimate stylomere almost straight over upper edge, curving distally over lower edge; terminal stylomere short, about one-third length of penultimate stylomere, stubby and bluntly rounded apically; scape unusually short, about equal in length to first stylomere. Female stylomeres moderately compressed laterally, entire style elongate, more slender than in male, tapering gradually, penultimate stylomere narrowing apically, terminal stylomere short, about half length of penultimate stylomere, tapering as in Fig. 5; basal stylomere relatively longer than in male, equal to combined lengths of 2 and 3; scape also proportionately longer than in male, slightly longer than basal stylomere. Antennal sensory vestiture in both sexes of two types that are clearly separated: a) dense covering of proclinate, setiform, probably mechanoreceptor sensilla, extending in male in a strip over entire dorsal surface of stylomeres 1–7 and over entire surface of 8, this strip very narrow because of strong lateral flattening of stylomeres; in female extending also over dorsal surface of 1–7 and entirely over 8, but in a broader strip and in a posteriorly widening area on basal stylomere; b) laterally and ventrally, surface of stylomeres with dense but pale vestiture composed of small, stout, anteriorly-curved sensilla set in round, refractive sockets, probably olfactory chemoreceptors.

Head (Fig. 1) not sexually dimorphic, with same autapomorphies in both sexes; in lateral view, head extended in horizontal body axis, projecting forwards and clearly separated from pronotum; occiput rounded, resulting in occipital foramen having a more postero-ventral position causing the paragular sclerites to be exposed on each side of foramen as projecting flanges beneath the head; clypeus projecting forwards prominently, as long as horizontal eye diameter.

Proboscis elongate, directed downwards, or in life directed obliquely backwards between the legs, about 3.3X length of mesonotum; due to horizontally extended form of head, proboscis emerges beneath anterior part of projecting clypeus beyond anterior margin of eyes. Syntrophium reaching to approximately 70% of labial length; labella elongate, narrowly cylindrical, close together, each labellum containing a single, undivided pseudotrachea occupying its entire internal length; labium curved posteriorly over its internal proximal end cephalad of basal attachment of syntrophium (Fig. 2), this curved basal part visible in fluid-preserved specimens (see also Stuckenberg 2002, Fig. 1) as a dark line which is produced by a pair of narrow, closely adjacent, parallel, sclerotised strips lying in the labial gutter along its entire length; integument forming posterior wall of labium with numerous minute, transverse corrugations (Fig. 2). Stipites of the form characteristic of genera with long proboscis, namely a pair of long, narrow sclerites embedded in membrane beneath head—normally they are parallel to each other, but in *irwini* they converge posteriorly towards occipital foramen and fuse together as in Fig. 3.

Male genitalia and abdomen. Abdomen slender, uniformly wide over much of length, widening over T7 and T8; T8 (Fig. 8) of plesiomorphic form, exposed, not withdrawn or infolded beneath T7, setose across entire exposed surface; epandrium (Fig. 9) arched, slightly wider than long, attached ventrally to dorsal bridge by two narrow, longitudinal sclerites set in membrane beneath epandrium; synsternite (Fig. 10) with broadly v-shaped posteromedian opening; dististyle short, stout, with deflexed point apically; dorsal bridge narrow, at each end with a dorsally extended arm on which epandrium articulates; aedeagus with strong lateral extensions which expand apically as in Figs 11, 12; a small, weak median keel present basally; ejaculatory apodeme an irregularly curved, internal rod.

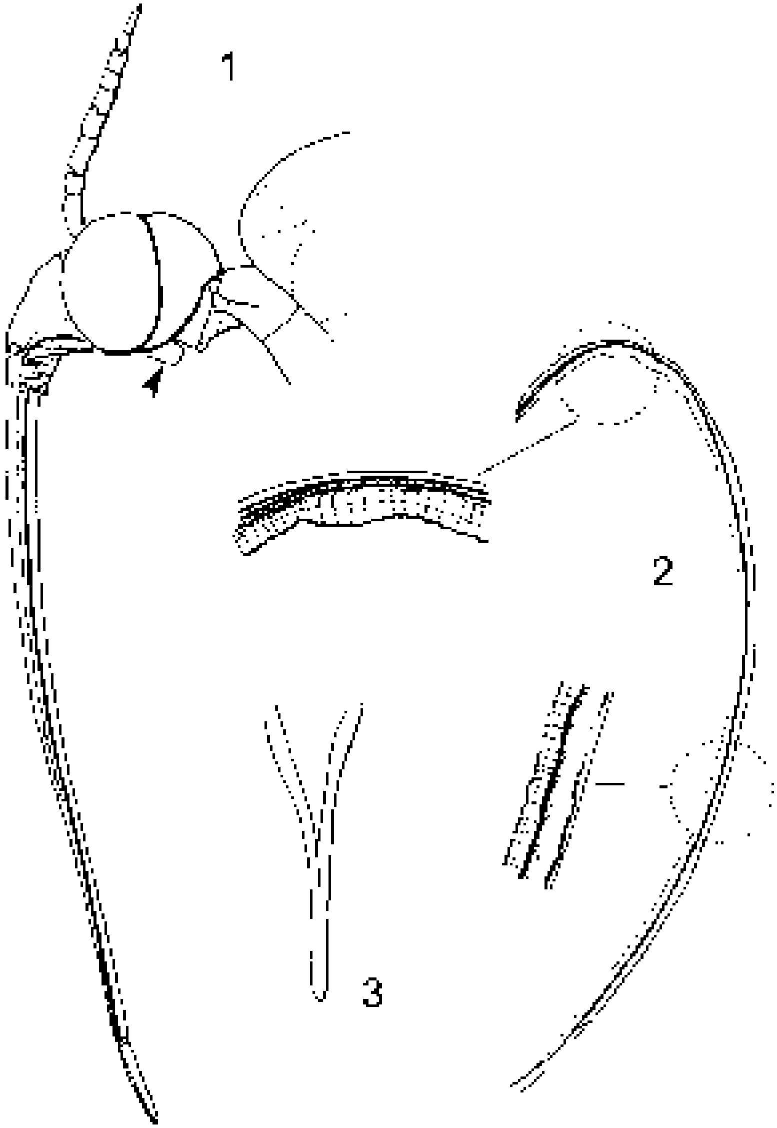
Female abdomen as previously illustrated (Stuckenberg 2002, Fig. 2). Spermatheca (Figs 13, 14) incompletely described and figured previously; mushroom-shaped, proximally concave with duct centrally inserted; distal surface with a central, circular aperture through which a short, subovate, eversible, membranous sac extrudes.

Isalomyia irwini Stuckenberg

Isalomyia irwini Stuckenberg, 2002: 3.

The original description was based on a moderately teneral female in ethanol. Pinned, more mature specimens of both sexes now enable a better description to be given. These are quite small vermileonids, slender, with elongate proboscis, large and prominent antennae, and strongly projecting clypeus. They are not pale yellowish as originally described, but glossy yellowish-orange or orange-brown, patterned on mesonotum and abdomen with dark spots.

Male: Mesonotum patterned as in female (Stuckenberg 2002, Fig. 2), pronotum with two longitudinal stripes, sternopleuron and mesopleuron shining brown; abdomen



Figs 1–3. *Isalomyia irwini* Stuckenberg. 1. Female head, lateral, the projecting paragular sclerite arrowed; internal recurved basal part of labium shown by dark line. 2. Complete male labium, anterior surface on right, recurved basal section at upper end; the arched form of exposed part is an artefact caused by detachment from the syntrophium which normally lies in the labial gutter and keeps the labium straight as in Fig. 1; dark line running internally over length of labium is produced by two narrow, parallel, sclerotised strips embedded in membrane of labial gutter; inset are two enlarged portions showing internal location of the strips which are closer to anterior surface basally where gutter is absent; corrugated posterior integument also shown. 3. Diagrammatic representation of form of stipital sclerites embedded in membrane under the head; they converge posteriorly and fuse.

yellowish-orange, T1 with two widely separated dark marks, other tergites extensively blackish laterally, with subtriangular markings narrowing towards midline where they join in poorly defined dark areas; shining white pruinescence anterior to dark markings on each tergite, most visible in oblique frontal view; T8 mostly shining blackish, T9 blackish centrally.

Both sexes: Exposed paragular sclerites (Fig.1, arrowed) glossy brown, contrasting with ashy-grey occipital pruinosity; parocciput present, exposed in dorsal view as a short, brownish, transverse flange above occipital foramen; wing shining, unpatterned except cell sc slightly brown; veins mostly dark brown; crossvein sc-r variably positioned, in most specimens about midway between humeral crossvein and origin of radial-sector (normal position in Vermileonidae), nearer to humeral crossvein in holotype and a few other specimens; cell m3 narrowly open to closed; crossvein m-cu present; radial-sector and basal section of R_{4+5} about equal in length.

Wing length: Male 6.5 mm, female 9.3 mm.

Material examined: 1 male, 1 female pinned, 2 females in ethanol: MADAGASCAR: Fianarantsoa/ Prov. nr Isalo Nat'l Park/ Dry Ravine S. of Interpret. Ctr./ 22.56254'S 45.38411'E 825m/ Date 8/15.ix.2001/ coll. ME Irwin, FD Parker. Collected as larvae, reared by BRS at Merrivale; emergence dates - 2 females 25.09.2002; female 29.05.2002, male 27.04.2002; in Natal Museum. 22 males, 2 females, in ethanol, same locality data, removed from Malaise trap that operated during 7–22.ix.2002. In Natal Museum.

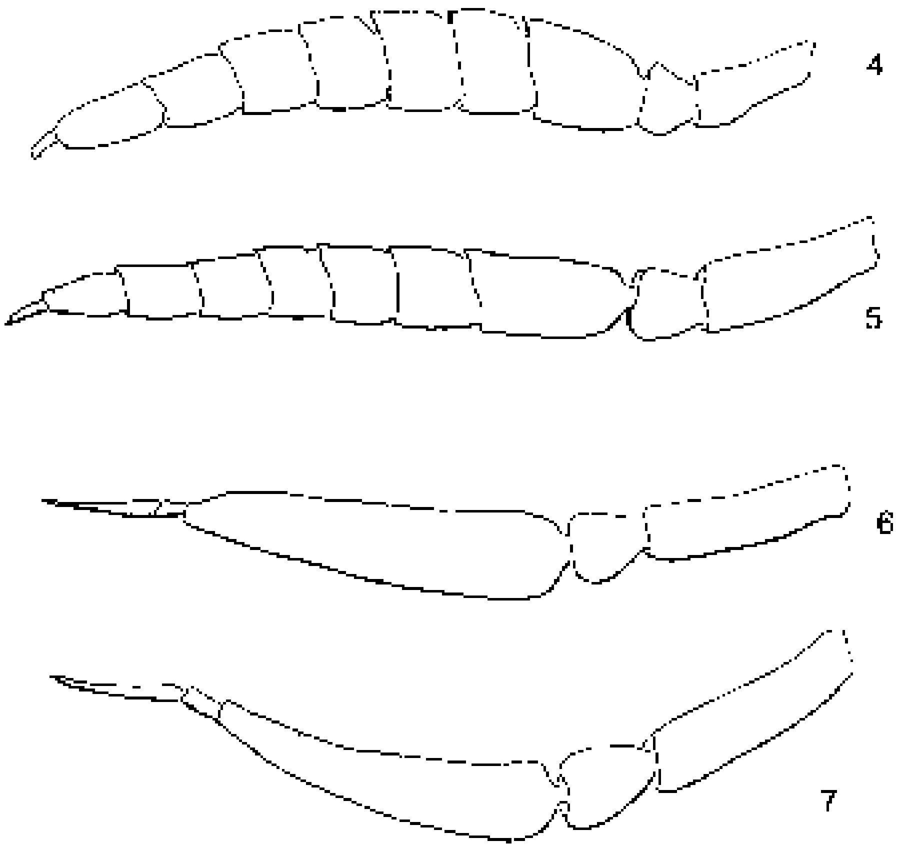
MOUTHPART MODIFICATIONS OF *ISALOMYIA*

The unique head form in *Isalomyia*—involving extension in the longitudinal axis and rounding of the occiput, with associated displacement of the paragular sclerites, posterior coalescence of the elongate stipital sclerites, and pronounced anterior protrusion of the clypeus—is part of a suite of modifications associated with adaptations of the proboscis. The remarkable form of the basal part of the labium, which recurves posteriorly within the head behind the attachment of the syntrophium and commencement of the pharynx, has the effect of preventing the entire proboscis from being extended forwards. Flexing of the proboscis obliquely backwards between the legs is structurally still possible, and is seen in many of the fluid-preserved specimens from the trap collection. Why the additional rigidity given to the proboscis by its basal curvature should be advantageous is unknown; it is also uncertain why the single pseudotrachea in each labellum has lost the apical bifurcation common in afrotropical vermileonids. Perhaps *irwini* has a close association with a plant having flowers of an unusual form, such as a particularly confined nectary. The plesiomorphic wing form suggests association with a floral biome in which no advantage lay in developing a capacity for hovering flight at flowers for nectar extraction (Stuckenberg 2000*b*, Fig. 22).

RELATIONSHIPS OF *ISALOMYIA*

In the original description of this genus it was recorded that its type species shares certain antennal and wing features with the Arabian species *Lampromyia umbraticola* Stuckenberg & Fisher, 1999. New information reported above suggests that these two species are sister-groups. The evidence is as follows:

1. Marked sexual dimorphism in antennal form (Figs 4–7). Although differing greatly in segmentation of the antenna, both species have the male antenna laterally flattened; this affects stylomeres 1–6 in *irwini* (Fig. 4) and the large postpedicel formed by fusion of stylomeres 1–6 in *umbraticola* (Fig. 6).
2. Development of only a very short terminal antennal mechanoreceptor in both sexes, despite large antennal size. In *irwini* (Figs 4, 5) the apex of the antenna is plesiomorphic, the apical segment being only moderately modified by apical narrowing. In *umbraticola* (Figs 6, 7) the postpedicel carries an apical style composed as usual of the two terminal stylomeres, of which the penultimate one is much the shorter, and the apical segment is narrow and tapers to a point. Normally in vermileonids, the two terminal stylomeres are coadapted to form an elongate, slender mechanoreceptor, nearly always longer than the preceding flagellar components combined.
3. Development of two forms of sensory vestiture, with clearly separated distribution of these forms on the flagellar components; the dorsal vestiture is a dense layer of



Figs 4–7. Antennae in lateral view; the shaded area on each one represents the distribution of a dense covering of proclinate setiform sensilla. 4 Male, 5 female, of *Isalomyia irwini* Stuckenberg; 6 male, 7 female, of *Alhajarmyia umbraticola* Stuckenberg & Fisher.

proclinate, setiform sensilla, lying as a continuous covering as shown schematically in Figs 4–7, more restricted to the dorsal surface in males. The lateral and ventral surfaces bear short, stout sensilla coeloconica that curve distally.

4. Spermatheca with a circular aperture centrally on distal surface, through which a subovoid membranous sac is extrudable.

Characters 1–4 above are synapomorphies; the following additional characters are shared by *irwini* and *umbraticola*.

5. Male T8 unmodified, exposed and setose across its entire width, not withdrawn beneath T7. This is the plesiomorphic condition, but it is uncommon in the afrotropical genera, many of which have T8 exposed only as small posterolateral lobes.
6. Dististyle short, stout, with deflexed apical point; this form is uncommon.
7. Wing form and venation very alike in the two species; petiole short, anal lobe not narrowed basally, crossvein m-cu present, radial-sector short. Probably these resemblances are plesiomorphies.

The original classification of *umbraticola* in *Lampromyia* was based on the presence of a bifid pseudotrachea in each labellum, but it was established subsequently (Stuckenberg 2000*b*) that this condition is not unique to *Lampromyia*. Erection of the following new genus for *umbraticola* is consequently required.

Genus **Alhajarmyia** gen. nov.

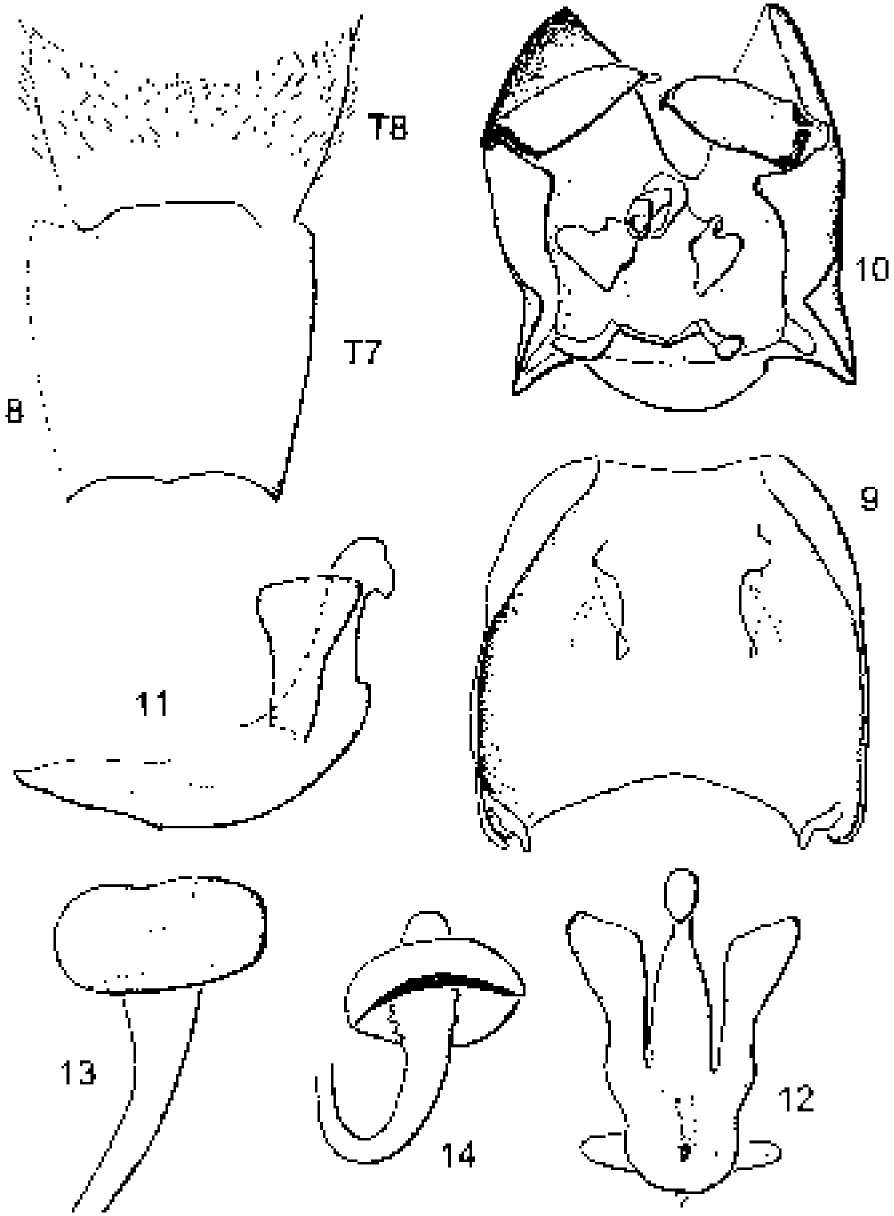
Type species: *Lampromyia umbraticola* Stuckenberg & Fisher, 1999: 129, by present designation.

Etymology: A combination of *Al Hajar*, the Arabic name for the Omani mountains where the type species occurs, with *myia* (G.) a fly; gender feminine.

A genus in the afrotropical monophylum of Vermileonidae, which is characterised by having an elongate, slender proboscis, a protruding clypeus, the maxillary palpi slender, clavate and straight with apical sensory pit, and the aedeagus as a sclerotised tube formed by fusion of paraphyses, with ejaculatory apodeme in the form of a slender, irregularly curved rod situated within this tube.

Description: With the characters 1–7 described above. Amber-yellow or orange-brown, slender flies with unpatterned wings and banded abdomen. Distinctive in form, segmentation and sensory vestiture of antennae (Figs 6, 7). Distinguished from *Isalomyia* Stuckenberg as follows: hind tibia thickened apically and wider than hind femur; the single pseudotrachea in each labellum is apically bifid; labium straight over its entire length; stipital sclerites subparallel to one another; aedeagus lacking lateral extensions; spermatheca subovoid (not mushroom-shaped); paragular sclerites not exposed in lateral view of head, but lying normally on each side of occipital foramen and confluent with adjoining surface of occiput.

Comparative notes: The thickened hind tibia occurs also in *Leptynoma* Westwood, 1876, *Perianthomyia* Stuckenberg, 1996, and *Vermilynx* Stuckenberg, 1995 of Southern Africa, but these three distinctive genera all have a trifid aedeagus and other strong apomorphies absent in *Alhajarmyia*. The monotypic South African genus *Namaquamyia* Stuckenberg, 2000 also lacks lateral extensions to the aedeagus, but shares no other significant features with *Alhajarmyia*.



Figs 8–14. *Isalomyia irwini* Stuckenberg. 8. Tergites 7 and 8, dorsal, setae on T8 shown. 9–12. Male genitalia. 9. Epandrium, ventral. 10. Synsternite with aedeagus, dorsal. 11. Aedeagus, lateral. 12. Aedeagus, posterior. 13. Spermatheca, lateral, membranous sac retracted. 14. Spermatheca, membranous sac everted.

BIOGEOGRAPHICAL IMPLICATIONS

It was unexpected that the only known Madagascan vermileonid should be related to a species confined to the upper reaches of the Hajar Mountains of Oman. That part of Arabia is an easternmost outlier of the Afrotropics, where palaearctic and oriental elements also occur (Larsen 1984; Holzel 1998). The Omani species is probably a relict, restricted by the aridity and high temperatures of the adjacent desert to a mesic zone in the altitude range of about 1800–2500 m, where a regular rainfall of about 150–350 mm p.a. occurs. A similar relict species occurs in the upper part of the isolated, prominent Brandberg massif of Namibia, which is surrounded by the arid gravel plains of the Namib Desert (Stuckenberg 2000*a*); the endemic *Perianthomyia monticola* Stuckenberg, 2000 is confined to a mesic zone at 1200–2000 m. Isolation of this species on the Brandberg would have resulted from Namibian desertification which began at the end of the Early Miocene (Pickford & Senut 1999).

To interpret the isolation of *umbraticola* in the Hajar Mountains, the period has to be identified when the ecological conditions that currently maintain its survival there occurred at much lower altitudes, allowing dispersal within Arabia. Range extension in Arabia appears not to have given afrotropical vermileonids entry to adjacent Levantine and Middle Eastern regions that came to unite with the Arabian sector of the African plate when continental drift closed the eastern Mediterranean in the terminal Miocene. This suggests that entry into Arabia might have been via a southern route, perhaps before opening of the relatively young Red Sea rift. Undiscovered species of *Alhajarmyia* may occur in the mountains of Yemen and in the Somali Peninsula.

The review by Maley (1996) of the vegetation history of the Saharan and Arabian areas since the Upper Cretaceous reveals this huge area to have been humid and well vegetated, with high rainfall in north-eastern Africa derived from the warm Tethys Sea. These conditions favoured the long-term presence of forests in which early angiosperms rapidly diversified and came to be dominant. Such conditions persisted through the Early Tertiary. In the Saharan region by the Middle Miocene there were lakes, swamps, permanent rivers, and a vast mosaic of forest patches and gallery forests intermixed with savanna. Environmental change in response to progressive aridification then began and intensified through the Late Miocene, leading to the Saharan and Arabian deserts developing from the Early Pliocene. Range restriction of vermileonids in Arabia could thus have commenced in the Late Miocene.

How the ancestral form of *Isalomyia* arrived in Madagascar is unknown. The summary by de Wit (2003) of geomorphological opportunities for vertebrates to gain access to Madagascar, emphasised that no land bridges or close proximity to other landmasses existed since the Late Cretaceous. De Wit considered that the perplexing problem of explaining the origin of enigmatic Madagascan vertebrates such as its lemurs, iguanas and primitive boid snakes, is still unsolved. For winged insects the explanation need not depend on continuous land connections: aerial dispersal may have occurred. The vermileonid fauna of the Canary Islands suggests this possibility: there are three endemic, allopatric species of *Lampromyia* Macquart, evidently derived from ancestral congeners in NW Africa (Stuckenberg 1971). These islands are volcanoes emerging from the sea; they have never been connected to one another by dry land, so aerial dispersal of vermileonid flies between them must have occurred over distances of 70 kms or more, depending on directions in which dispersal occurred.

The ancestor of the *Isalomyia* lineage may have been derived from East Africa, possibly from old fault-block mountains in Tanzania. Dispersal from an East African ancestor could also have produced the *Alhajarmyia* lineage in Arabia. How the sea gap between Africa and Madagascar could have been crossed, other than by extended aerial dispersal over at least 400 kms, is uncertain, but could have involved oceanic island chains such as the Comores which are of Late Cenozoic volcanic origin (10–15 Ma; de Wit 2003). There are also chains of small islands to the north of Madagascar, which are associated with submarine ridges and rises whose elevations may have varied through tectonic activity or changes of sea-level. A more complex scenario could involve the Seychelles islands which are vestiges of a microplate that separated from India in the Late Cretaceous (de Wit 2003). A study by Johanson (2002) of the caddisfly genus *Helicopsyche* (Trichoptera, Helicopsychidae) shows that the two most primitive species occur in Madagascar and are the sister-group of two other relatively primitive species in the Seychelles. In turn, the sister-group of these four island species is constituted by more apomorphic species in East Africa, particularly in the Eastern Arc Mountains of Tanzania. In view of the wealth of endemism known to occur among invertebrates in those mountains, the presence of vermileonids there would be no surprise.

ACKNOWLEDGEMENTS

This study was made possible by a consignment of live wormlions and a catch of *Isalomyia* flies from a trap, all from the type locality, sent by Dr Mike Irwin; his enthusiastic and effective support of my studies on vermileonids is much appreciated. I am grateful to Dr Hans Ulrich for advice regarding the nomenclature of occipital sclerites. Thanks are due to my colleagues Dr Jason Londt and Dr David Barraclough for reviewing a draft of this manuscript, and to Ms Catherine Conway for artwork and technical support.

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